

Biomass allocation and assimilation efficiency of natural *Tilia amurensis* samplings in response to different light regimes

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Abstract Biomass allocation and assimilation efficiency of natural Amour linden (*Tilia amurensis*) samplings in different light regimes were analyzed in the paper. The results showed that shoot increment of samplings in gap was the highest and that of samplings under canopy was the least. Samplings in gap expressed apical dominance strongly but samplings in full sun and under canopy behaved intensive branching. Lateral competition or moderate shading was favored to bole construction. The patterns of biomass allocation of samplings in different light environment were rather similar. The biomass translocated to stem was more than that to other organs, and about one half of photosynthate was used to support leaf turn over. On the contrary, photosynthates of samplings in full sun were mostly consumed in leaves bearing and energy balancing. The carbon assimilation for leaves of samplings in gap was the most efficient, and more carbons were fixed and translocated to non-photosynthetic organs, especially to stemwood.

Key words: *Tilia amurensis*, Shoot growth, Biomass allocation, Assimilation efficiency of leaf, Light environment

Introduction

Amour linden (*Tilia amurensis*), an important component of naturally mixed broad-leaved-Korean pine community in eastern mountain area of Northeast region of China, is one of main species used as high quality veneer and cabinetworking timber. But the amount of natural linden resources with high quality was sharply decreased with long historical exploitation without planting so that little linden timber have been supplied in timber market.

Belonging to associating species in climax community in the region, the species has a big faculty. But the germinating rate of seeds is rather low because seeds with long fruit-stalk and flower anthodium were not being buried in soil (Nie *et al.* 1992). Many highyield plantations have been built to compensate the loss of natural resources, but few of them were worthy plantations. Few studies had been reported such as management measure, growth status of young linden plantation (Zhou *et al.* 1986; Wang *et al.* 1991; Shi *et al.* 1991; Hu *et al.* 1991) and population ecology (Nie *et al.* 1992). However the successfully cultural measures of stem form in the plantation have not been formed, most of individuals of plantation have multi-stems or grow shrubberily. It is worthy that stem form of naturally established samplings in old growth forest is very well and the bole is almost single. Thus the purposes of the paper is try to provide some theoretical references for stem form culture of the

linden plantations by analyzing the growth and biomass allocation status of natural samplings in old growth forest.

Materials and methods

Study sites

The investigated stand in Dongsheng Forest Farm of Lushuihe Forest Bureau locates on northwest slope of Changbai Mountain, Jilin Province (127° 47' E, 42° 31' N). The stand, a typically mixed forest of mature broad-leaved Korean pine community, is composed of Korean pine (*Pinus koraiensis*), *Abies hollophylla*, *Acer mono*, *Tilia amurensis* and some mesophaneropytes species. Understory shrubs mainly consist of *Eurymus macropterus*, *Syringa reticulata* var. *mandshurica*, *Acanthopanax senticosus*, *Prunus manimowiczii*. And land-flora species include *Hippochaete hyemale*, *Brachybotrys pariformis*, *Carex callitrochos*, *Dryopteris crassirhizoma* and so on. The topography being occupied by the stand is mountain terrace whose elevation is 750 m. The annual average temperature is 2.67 °C, the annual total sun-hour 2015.3 h, annual precipitation is 871.6 mm, and annual total evaporation for 1166.4 mm. The active accumulative temperature which is $\geq 5^{\circ}\text{C}$ is 1527 °C per year, and the active accumulative temperature which is $\geq 10^{\circ}\text{C}$ only is 744 °C per year.

Data collection

Light is one of the most important factors affecting growth of linden samplings. For the sake of conven-

ience to analysis, the site of samplings was classified into 3 categories: grass and shrub land of forest edge referencing to full sunshine, gap and under canopy site referencing to shade gradients. The linden samplings whose ages are from 4 to 12 year-old and whose heights from 80 cm to 200 cm were selected and harvested in each growing site. The annual extensive growth of all branches was measured. And successive growth increments were distinguished by bud scar. The total height, crown length, average crown diameter, projected crown area, and stem diameter at the root collar were measured in the field for each sampling. 50 blades in different layers of target sampling canopy were sampled to measure leaf area, specific leaf area by means of blade discs method. All leaves and branchlets in terms of bifurcations on main branch were counted. Samples were dried at 80°C for 48 h in oven so as to estimate dry biomass of each organ. Stem analysis data were collected from 120 samplings in the early August of 1997.

Statistical analysis

The assimilation efficiency of organs was defined as organ biomass per leaf area per year ($\text{g}/\text{m}^2 \cdot \text{a}^{-1}$). The index of leaf area (ILA) was defined as total leaf area or crown area. The increment of each organ biomass ($\text{g} \cdot \text{a}^{-1}$) was standardized using sampling age for the sake of heterogeneity of sampling age. The ratio of terminal shoot to lateral shoot was calculated as increment of terminal shoot to average extension of lateral shoot. The biomass of lateral branch included shoot biomass. Relationships between variables were calculated using linear regression analysis. The markedness test of coefficient of correlation was performed using *t*-test method.

Results

Shoot increment

Shoot increment was markedly affected by growing environment that the growth of terminal and lateral shoot of samplings in gap was the highest, and that of samplings under canopy was the lowest in every year (Fig.1, Fig.2). The shoot increment of samplings in shade environment increased with light intensity. It indicated that light harvest of samplings is one of the key factors affecting shoot growth. The increment of terminal shoot of sampling under canopy, which subjected to lateral suppression slightly, was similar to that of sampling growing freely in full sun (Fig.3, Fig.4). It meant that lateral competition promoted bole formation. The shoot increment of samplings in full sun site was not higher than that of the sampling in gap. The results showed that high light was not favorable to shoot elongation. The intensity of apical

dominance in terms of the value of increment of terminal shoot to lateral shoot supported the viewpoint also (Table 1).

Table 1. The increment ratio of terminal shoot to lateral shoot of samplings exposed to different light regimes

Site	Year			
	97	96	95	94
Full sun	1.54	1.76	2.28	2.09
Lateral pressure	1.71	1.87	1.81	2.54
Growing freely	1.40	1.67	2.75	1.63
Under canopy	2.37	1.97	2.32	2.28
Lateral pressure	2.57	2.17	2.53	2.01
Severe shade	2.06	1.60	2.05	2.89
Growing freely	2.49	2.54	2.04	1.54
Gap	2.28	2.04	2.12	2.14
Lateral pressure	2.35	2.16	2.17	2.22
Shade	2.29	2.03	1.80	2.05
Growing freely	2.17	1.86	2.12	2.53

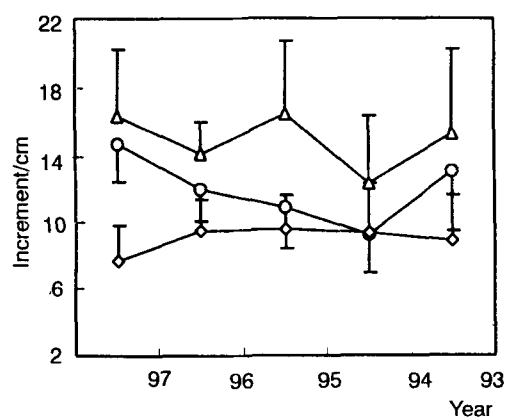


Fig. 1. Annual increment of branch exposing to different light regime

—△— Gap; —◇— Under canopy; —○— Full sun

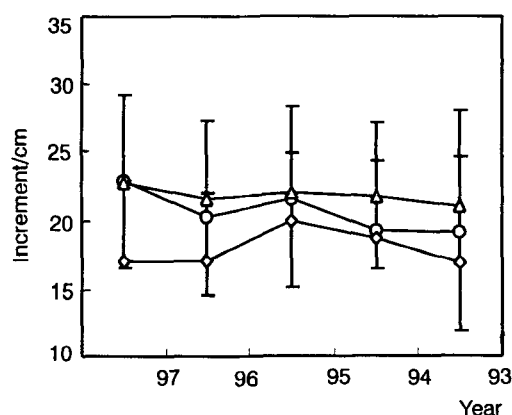


Fig. 2. Annual increment of bole exposing to different light regimes

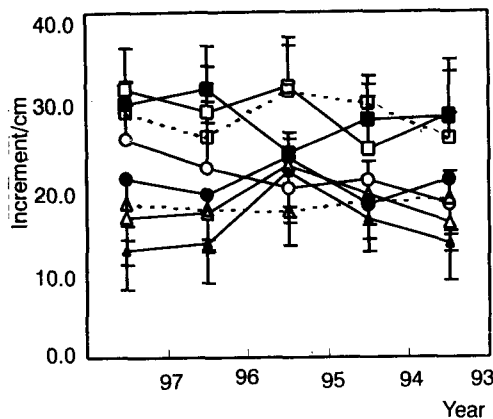


Fig. 3. Influence of competition on terminal shoot increment

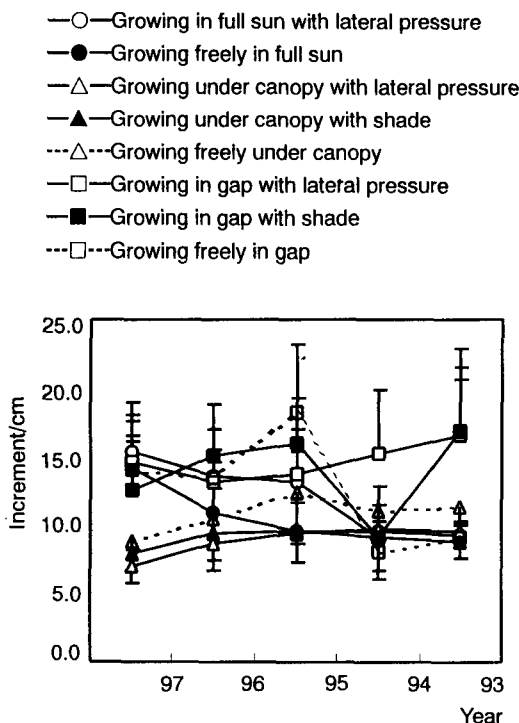


Fig. 4. Influence of competition on lateral shoot increment

- Growing in full sun with lateral pressure
- Growing freely in full sun
- △— Growing under canopy with lateral pressure
- ▲— Growing under canopy with shade
- △--- Growing freely under canopy
- Growing in gap with lateral pressure
- Growing in gap with shade
- Growing freely in gap

Apical dominance of samplings with lateral suppression in full sun site was stronger than that of samplings growing freely so did samplings growing in gaps. The intensity of apical dominance of samplings with differently extent shadiness gradually enhanced with increase of sampling age. The samplings in full

sun process the opposite way. Shoot elongation was the highest for samplings growing freely under canopy. But severe shadiness might retard shoot extension. It suggested that lateral shadiness, or lateral competition, to samplings could promote bole extension.

Biomass allocation

In general, the pattern of biomass allocation of the linden samplings in any sites was quite similar (Fig. 5) and supported by the biomass allocation of several *Quercus* species (Callaway 1992). As most temperate broad-leaved samplings and seedlings, natural established samplings of the linden allocated more fixed carbons to bole and root construction, and less carbons to branch except maintenance of leaf metabolism. Samplings with lateral competition were assigned more carbons to bole than samplings growing freely. This indicated that lateral competition might be favorable to bole formation. Samplings with weak competition or shade produced more leaves. Root, especially lateral root, is the organ for plant to absorb water and mineral. The biomass allocated to lateral root for samplings in full sun was more than that in shade site since water suppliation was always the restrict factor for plant growth in high light environment. Samplings in full sun needed to evaporate more water than samplings in shade site to balance absorbed energy in growing season. Thus developed lateral root was very important for samplings to gain sufficient water in full sun. Furthermore, apical dominance was expressed very well in biomass allocation of linden samplings. For instance, sampling with lateral competition assigned more biomass to bole, and less biomass to other organs in any sites (Fig. 6), and samplings without competition assigned more biomass to root construction.

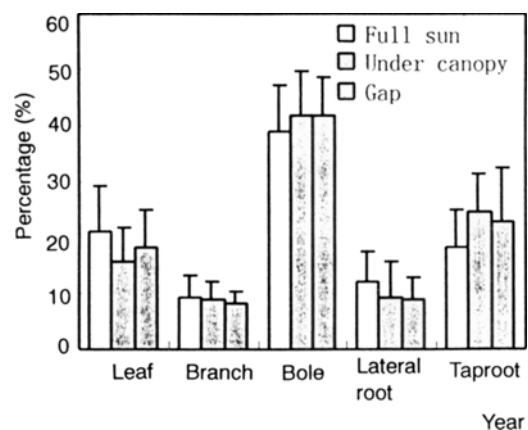


Fig. 5. Biomass allocation of samplings in different sites

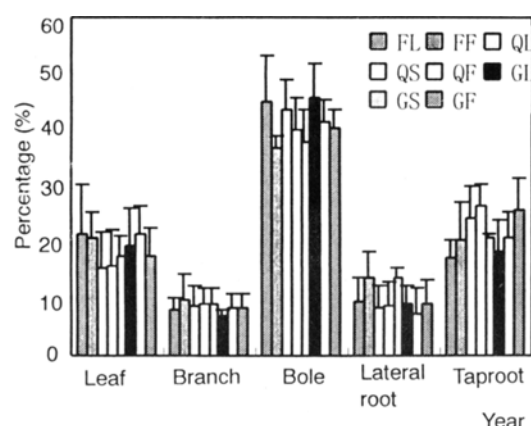


Fig. 6. Influence of competition on biomass allocation

FL--Growing in full sun with lateral pressure

FF--Growing freely in full sun

QL--Growing under canopy with lateral pressure

QS--Growing under canopy with shade

QF--Growing freely under canopy

GL--Growing in gap with lateral pressure

GS--Growing in gap with shade

GF--Growing freely in gap

Assimilation efficiency of leaf

Leaf, the only organ to assimilate carbon it carbohydrate, is the most sensitive organ to different inten-

sity of radiation. Thus biomass or the number of leaf is, at least for the linden, not reasonable variable to evaluate productivity of samplings in different light regimes. So absolute increment of biomass and the assimilation efficiency of leaf in terms of annual biomass accumulation of organs or whole individual in one unit leaf area were introduced.

About one half of carbons assimilated by the linden sampling was used to support leaf metabolism in investigated area, and only about one quarter of fixed carbons was used to construct stem (Table 2). More carbons were assigned to lateral root than to taproot. The results showed that constructive investment of samplings to absorbing section of root was gradually enhanced with increase of sampling age. Though biomass accumulation of leaf of samplings in gap was less than that of samplings in full sun. Leaf vigor in carbon assimilation was much higher, which expressed as that sampling in gap cumulated more biomass than that in other light environment at the same as cost of leaf area. The leaf area ratio of samplings in gap was the least (Table 2). The average index of leaf area (AILA) of samplings in full sun is beyond 1. This indicated that less leaf overlapping occurred in samplings in gap. And it suggested that the arrangement of leaf in crown of samplings in gap was more favorable to radiation acceptance.

Table 2. Increment of different organs and assimilating efficiency of leaf of samplings in different sites

Parameters	Light gradients						P-value
	Full sun		Under canopy		Gap		
	Annual average increment of different organs /g•a ⁻¹						
Leaf	30.6	(11.4)**	17.0	(10.1)	27.4	(13.4)	0.002
Mass of lateral branch	2.2	(1.0)	1.4	(0.8)	1.8	(1.0)	0.023
Mass of bole	11.0	(4.8)	7.0	(3.4)	11.7	(8.8)	0.021
Mass of root	5.9	(2.2)	3.4	(1.2)	5.7	(2.7)	0.024
Taproot	3.2	(1.0)	2.7	(2.3)	3.6	(3.2)	NS
	Assimilating efficiency of leaf /g•m ⁻² •a ⁻¹						
Leaf	159.6	(46.2)	112.9	(32.0)	147.2	(28.4)	0.000 4
Lateral branch	12.8	(7.2)	8.0	(3.7)	10.7	(3.7)	0.046
Bole	51.8	(21.2)	37.6	(16.6)	57.0	(15.6)	0.004
Lateral root	23.7	(11.2)	17.8	(8.5)	28.3	(14.4)	0.024
Taproot	15.7	(7.5)	8.6	(6.3)	14.3	(5.5)	0.004
	Other variables						
Leaf area ratio (cm ² •g ⁻¹)*	42.6	(13.4)	51.4	(16.4)	41.7	(9.4)	0.048
Leaf density (blades /1-m branch)	48.2	(7.1)	40.9	(6.7)	38.3	(7.1)	0.002
Index of leaf area (ILA)	1.2	0.47	0.7	0.19	0.8	0.33	0.013
Branchlet density (branchlets/1-m branch)	5.9	(2.4)	8.2	(2.2)	5.8	(1.9)	0.000 1
Branch density (branches/1-m bole)	8.8	(3.5)	7.4	(2.3)	6.5	(2.0)	0.017

Note: * Leaf area ratio is the value of leaf area requirement for producing one unit biomass.

**--Data in brackets are standard deviation.

Conclusions and discussion

Shoot increment

Field experiments demonstrated that the growth of tree seedlings could be simultaneously limited by both of light and soil resources (Latham 1992). But the balance of the effect of aboveground and belowground competition depended on the effects of site quality on the overall availability of soil resources (Putz and Canham 1992; Canham *et al.* 1996) and light. In the site without fierce competition, light availability became the mainly limited factor. Shoot extension of the linden sampling in moderate radiation site was the activist in investigated area but lateral and terminal shoot growth was decreased in severe shade site. The results differed slightly from some shade species whose elongation of branch increased with enhances of shadiness (Chapin *et al.* 1987). And it also differed from some shade-tolerant trees whose height growth and mean lateral growth of samplings increased in response to increased PPFD (Beaudet and Messier 1998). But it was consistent with Igboanugo (1990) who found that increment of terminal shoot of *Quercus petraea* seedling, a shade-tolerant broad-leaved species, exposed to moderate radiation was the highest. The reason was partially that high light often restrained leaf of shade tolerants from efficiency of carbon assimilation and subjected to photo-inhibition or decreased of water use efficiency for strong evaporation. In exposed environment, response in the length of axes was more likely to be caused by the photo-inhibition of cell wall expansion at high light intensities also (Cornelissen 1993). Leaves of sampling in full sun and gap mainly displayed on long-branches whereas leaves of samplings under canopy arranged on branchlets. The branchlet density of the linden samplings growing under canopy was 40% more than that of samplings in other site (Table 2). It revealed that leaves of samplings, which subjected to shadiness modulated arrangement by improving branchlets development in order to enhance the light availability. Thus most of carbon were consumed by formation of branchlets and leaves instead of by stem construction. The weakening of apical dominance of samplings in full sun resulted in that large number of lateral buds were released and developed into branches. Thus the result led up to decreasing the increment of terminal shoot.

Biomass allocation

Allocation of biomass to leaves, stems, and roots did not vary obviously within species in different shade environments (Callaway 1992; O'Connell and Kelty 1994). But most proportion of photosynthate

synthesized in leaves of the linden sampling was translocated to bole formation, followed by taproot and leaf consuming while least carbohydrates was assigned to lateral roots and branches except leaves (Fig. 5). In the same environment category, more biomass was allocated to bole, and then lateral roots and branches, and biomass distributed to taproot was following the oppose way. Moderate shadiness or lateral competition was favored to biomass accumulation, especially to stemwood formation. For a wide variety of plants, roots accounted for 50%~80% of annual dry matter production (Chapin *et al.* 1987). And the cost of producing a unit of root biomass was similar to that for other tissues. Thus a large biomass allocated to roots represented a substantial carbon cost. But for the linden samplings, large quantity of carbon was used to support leaves production. The results indicated that the linden samplings had more resources demands, especially radiation, to establish themselves. Photosynthates translocated to aboveground was remarkably more than to belowground (55%, 74% and 64% for full sun, under canopy and gap respectively), which implied that the linden samplings trended to select shade-avoidance strategy although belonged to shade-tolerance.

Assimilation efficiency of leaf

Assimilation efficiency of leaf of samplings in gap was the highest though total annual biomass accumulation per leaf area of samplings exposed to full sun was higher than that of samplings in gaps (Table 2). Because leaf area ratio of samplings in gap was the least and total annual biomass accumulation of non-assimilation organs of samplings in gap was the highest. The ratio of aboveground biomass to root biomass of samplings in gap was higher than that of samplings in full sun, which could also explain above-mentioned conclusion.

Based on aforesaid discussions, gap and moderate shadiness site were the most favorable environments to construction of the linden samplings. The samplings in full sun or severe shadiness environment would develop more branches or produce less biomass. The multi-stems phenomenon of samplings in young linden plantation might be related to phytohormone harmony caused by high radiation. Of cause freezing harm was not excluded. From the view of light environment, mixed plantation in logged area or regenerating under canopy before logging may be good measures to promote bole development for the sapmlings. And remaining herbs or shrubs properly may be also favor the linden samplings to form qualified stemwood by means of lateral suppression of shrubs and herbs in young plantation management.

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